

1 abmR: an R package for agent-based model analysis 2 of large-scale movements across taxa

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6 Benjamin Gochanour^{1,2,*}, Javier Fernández-López³, Andrea Contina⁴

7 ¹ Corix Plains Institute, University of Oklahoma, Five Partners Place, 201 Stephenson Parkway, Norman, OK
8 73019, USA

9 ² Oklahoma Biological Survey, University of Oklahoma, 111 East Chesapeake Street, SC Building 134,
10 Norman, OK 73019, USA.

11 ³ University of Massachusetts Boston, Department of Biology, Integrated Sciences Complex, 100 Morrissey
12 Blvd., Boston, MA 02125

13 ⁴ University of Colorado Denver, Department of Integrative Biology, Science Building 2074, Denver, CO
14 80217, USA

15

16 *Corresponding author

17 *E-mail: gocha001@umn.edu

18 Benjamin Gochanour ORCID: 0000-0002-0950-1739

19 Andrea Contina ORCID: 0000-0002-0484-6711

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29 **Abstract**

30 1. Agent-based modeling (ABM) shows promise for animal movement studies.

31 However, a robust, open-source, and spatially explicit ABM coding platform is
32 currently lacking.

33 2. We present abmR, an R package for conducting continental-scale ABM simulations
34 across animal taxa. The package features two movement functions, each of which
35 relies on the Ornstein-Uhlenbeck (OU) model.

36 3. The theoretical background for abmR is discussed and the main functionalities are
37 illustrated using two example populations.

38 4. Potential future additions to this open-source package may include the ability to
39 specify multiple environmental variables or to model interactions between agents.

40 Additionally, updates may offer opportunities for disease ecology and integration with
41 other R movement modeling packages.

42 **Keywords:**

43 Animal migration; R programming; computer simulations; ecology

44 **Abbreviated Title:** agent-based models in R

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51 **1. INTRODUCTION**

52 Animal movement is a complex behavioral trait that affects the survival of populations and
53 species across taxa (Berg, 1983; Dingle, 2014). Long- and short-distance movements can be
54 predictable, allowing populations to take advantage of seasonal food resources (e.g.,
55 migration), or more opportunistic, such as in the case of dispersal behaviors aimed at
56 avoiding predators or finding potential mates (Giuggioli & Bartumeus, 2010). Thus, wild
57 animals make decisions often based on environmental cues that lead to movement patterns
58 characteristic of different populations across the landscape (Nathan et al., 2008; Dodge et al.,
59 2014). However, obtaining a comprehensive understanding of large-scale animal movement
60 behavior and population occurrence under climate change scenarios or habitat loss has proven
61 to be a challenge (Araujo & Guisan, 2006). Moreover, while the research toolbox in
62 movement ecology studies has seen a considerable expansion over the last two decades due to
63 technological advancements of the tracking devices and molecular markers (Cushman and
64 Lewis, 2010; Williams et al., 2020), the limitation of scaling up individual data to population-
65 level inferences is still a substantial obstacle (Hawkes, 2009; but see Holdo & Roach, 2013).
66 A promising research approach that may overcome the limitations of wildlife movement
67 studies hindered by small sample sizes is represented by computer simulations within an
68 Agent-based Modeling (ABM) framework (Tang & Bennett, 2010; Bridge et al., 2017).
69 The core principle of ABM is to simulate a set of entities, called agents, which are defined by
70 intrinsic properties as well as behavioral rules governing their interactions with the
71 environment (Grimm & Railsback, 2013). That is, agents are described by their inherent
72 attributes while dynamically interacting with external conditions such as the co-occurrence of
73 other agents and/or changing features of their environmental setting . Thus, ABM has found
74 applications in many study areas including biology, disease risk, social sciences, and

75 economics (Polhill et al., 2008; Grimm & Railsback, 2013; Kilmek et al., 2015; Willem et al.,
76 2017) with the unifying goal of investigating and predicting the dynamics of complex
77 systems (Grimm et al., 2005). In particular, wildlife studies have adopted the ABM approach
78 to simulate population growth, reproduction, mortality rate, energy budget, and migration
79 ecology, just to cite a few (Brown & Robinson, 2006; Lustig et al., 2019; Aurbach et al.,
80 2020; Goldstein et al., 2021). However, we currently lack a robust and spatially explicit ABM
81 coding platform for the implementation of large-scale animal movement investigations (but
82 see Thiele et al. (2012) or Chubaty and McIntire (2021)). Here we present a novel ABM
83 framework in the R programming language for applications in animal behavior and
84 movement ecology broadly defined.

85 **2. PACKAGE OVERVIEW**

86 abmR allows for both computation and visualization of agent movement trajectories through
87 a set of behavioral rules based on environmental parameters. The two movement functions,
88 `moveSIM` and `energySIM`, provide the central functionality of the package, allowing the
89 user to run simulations using an Ornstein-Uhlenbeck movement model (Uhlenbeck &
90 Ornstein, 1930; hereafter OU). Additional functions provide a suite of visualization and data
91 summarization tools intended to reduce the effort needed to go from results to presentation-
92 ready figures and tables (Table 1). The package is currently available as a Github repository
93 (<https://github.com/bgoch5/abmR>), but has been submitted to the Comprehensive R Archive
94 Network (CRAN) to facilitate broader access and usage.

95

Function	Usage
moveSIM	Runs agent-based model movement simulations based on environmental data
moveVIZ	Creates a plot or table of moveSIM() results
energySIM	Runs agent-based model movement and energy budget simulations based on environmental data
energyVIZ	Creates a plot or table of energySIM() results
tidy_results	Prints results from moveSIM() or energySIM() in an easier-to-read table
get_ex_data	Downloads data that is used in examples in vignette and documentation
as.species	Creates object of class 'species' for input into moveSIM() or energySIM()

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97 **Table 1.** Functions contained in the abmR package (v. 1.0.1). For more complete function

98 descriptions, consult the abmR manual.

99 Both movement functions used by abmR rely on the same OU model approach summarized

100 below. Given current agent location (x_t, y_t), agent location at the subsequent timestep ($x_{t+1},$

101 y_{t+1}) is modeled according to the following equations:

$$102 \quad x_{t+1} = x_t + \sigma * Z + \phi_x * (\omega_x - x_t) \quad (1)$$

$$103 \quad y_{t+1} = y_t + \sigma * Z + \phi_y * (\omega_y - y_t) \quad (2)$$

104 Here, σ is the randomness parameter from the Brownian motion process that serves as a

105 multiplier on the error term Z , a single random number drawn from the Normal(0,1)

106 distribution. In addition, ϕ_x and ϕ_y are movement motivation or attraction strength for the OU

107 process in the longitude and latitude coordinates, respectively, while ω_x and ω_y are optimal x

108 (longitude) and y (latitude) coordinates, respectively. It is assumed that the origin point ($x_1,$

109 y_1) is known. The OU model given in (1) and (2) performs similarly to a spring-coil. Greater

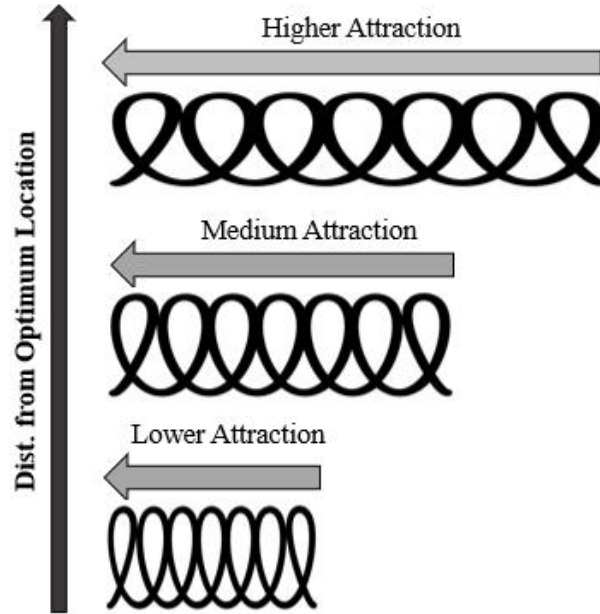
110 distance from optimal coordinates ω_x and ω_y acts like a compressed spring to propel distant

111 agents towards ω_x and ω_y . On the other hand, agents closer to ω_x and ω_y will travel a shorter

112 distance on that timestep. However, the amount of movement also depends on ϕ_x and ϕ_y ,

113 because these motivations serve as a multiplier on $(\omega_x - x_t)$ and $(\omega_y - y_t)$, respectively

114 (Eqns. 1 and 2).



115

116 **Figure 1.** The OU model given in (1) and (2) performs like a spring-coil: agents further from their
 117 target location experience higher attraction (and travel further), while agents closer to their destination
 118 experience lesser attraction (and travel less far).

119 Both movement functions allow the user to optionally specify two morphological parameters.

120 These morphological parameters are used to compute adjusted agent motivations ϕ_x and

121 ϕ_y from user-specified motivations ϕ_{x0} and ϕ_{y0} .

122
$$\phi_x = \phi_{x0} + (\pm 0.1 * ((a - \mu_a) / S_a)) + (\pm 0.1 * ((b - \mu_b) / S_b)) \quad (3)$$

123
$$\phi_y = \phi_{y0} + (\pm 0.1 * ((a - \mu_a) / S_a)) + (\pm 0.1 * ((b - \mu_b) / S_b)) \quad (4)$$

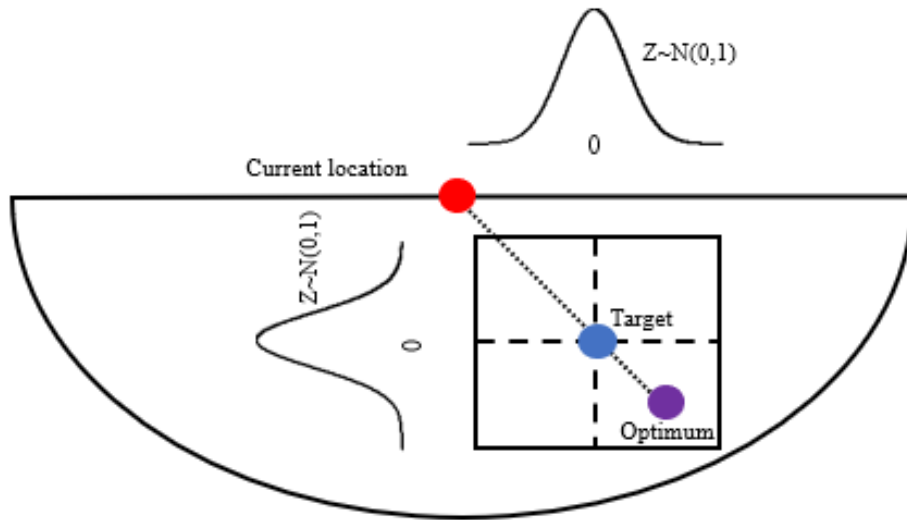
124 Here, a , μ_a , and S_a represent the observed value, population mean, and population standard
 125 deviation for the first morphological parameter, respectively, while b , μ_b , and S_b represent

126 analogous quantities for the second morphological parameter. The sign on the numerical
 127 constant 0.1 depends upon the hypothesized effect of each morphological parameter on agent
 128 movement. If increasing values of the parameter lead to increasing motivation, a positive sign

129 should be used, and if increasing values of the parameter lead to decreasing motivation, a
130 negative sign should be used. For example, if one hypothesizes that increasing mass leads to
131 less movement motivation, a negative sign should be used for this parameter. The biological
132 basis for including morphological parameters as a multiplier on motivation relies on previous
133 research showing that individual and population intrinsic morphological characteristics affect
134 migration speed, distance, and timing in many species (Alerstam, 1993; Hedenström, 2008).

135 While the two movement functions are distinct (see below), each follows the same basic two
136 steps. The first, large-scale searching, is illustrated in Fig. 2. This step finds the ‘optimum’
137 location for each agent (ω_x and ω_y coordinates from Eqns. (1) and (2)), that is, the geographic
138 point with the optimal environmental raster value in a semicircular search region depending
139 on movement orientation. For `moveSIM`, this optimal raster value is supplied directly, while
140 for `energySIM` it is the average of the lower and upper bounds of a user-specified optimum
141 range. The optimum value or range of values specified depends on the modeling scenario and
142 the type of environmental raster that is used (e.g., vegetation, temperature, etc.).

143 Agents will move toward the selected optimum location. However, if the attraction strength
144 (ϕ_x and ϕ_y in Eqns. (1) and (2)) is less than 1, agents will have a ‘target’ location short of the
145 optimal location. Agents will move towards this target location with some error, which is
146 generated by sampling from the normal distribution and multiplying by σ , as specified by the
147 user (In Fig. 2, σ is 1). Because the support of the normal distribution consists of all real
148 numbers, large deviations from the ‘target’ point are possible. However, because the normal
149 distribution has low density at the extreme tails, outcomes are most likely to fall within a
150 certain rectangle of the target, as illustrated in Fig. 2. This first step corresponds to the OU
151 model of Eqns. (1) and (2).



152

153 **Figure 2.** Illustration of large-scale searching specified by the OU model of Eqns. (1) and (2). Agents
154 find an ‘optimum’ location within the semi-circular search region and then a ‘target’ location that lies
155 on the line between the ‘current location’ and the ‘optimum’ location. If there is a tie between
156 multiple potential ‘optimum’ cells, one is randomly selected from the list of tied cells to serve as the
157 optimum. Random error is added by sampling from a $Z \sim N(0, 1)$ distribution. Here, $\sigma = 1$ and $\phi_x =$
158 $\phi_y < 1$, where σ is the multiplier on the random error and ϕ_x and ϕ_y are the motivations in the x and y
159 directions, respectively. Bounding box represents the most probable samples from the $N(0,1)$
160 distribution.

161 The second step is small-scale searching. Here, agents select the ‘best’ of the 8 neighboring
162 cells (queen’s case or Moore neighborhood) after performing step 1, discussed above and in
163 Fig 2. Again, ‘best’ here means the cell with environmental raster value closest to the agent’s
164 user-defined optimum range. These two steps are then repeated for each timestep until the
165 agent dies or proceeds through all timesteps. For the `moveSIM` function, agent death occurs
166 when agents fail to achieve suitable environmental raster values for more than a user-
167 specified number of consecutive timesteps. Here, what constitutes a ‘suitable’ cell is
168 determined by the optimum value and an allowable deviation proportion, both also specified

169 by the user. For the `energySIM` function, agent death occurs when energy reaches zero. For
170 both functions, users may choose to disable agent mortality. In the following subsections, we
171 present the differences between `moveSIM` and `energySIM` functions and their underlying
172 algorithms.

173 **2.1. Simulation function: `moveSIM`**

174 The function `moveSIM` runs an OU movement simulation based on environmental conditions
175 provided by the user (e.g., raster), optionally including agent mortality and adjusted
176 motivation according to user-specified morphological parameters. The function operates
177 according to the following algorithm. Here, terms in *italics* are `moveSIM` function arguments
178 (see Table 2).

179

Argument	Function	Usage
replicates	M, E	number of agents to model
days	M, E	number of timesteps
modeled_species	M, E	Species object from <code>as.species()</code>
env_rast	M, E	Environmental raster
optimum	M	Optimal environmental value
optimum_lo	E	Lowest optimum environmental value
optimum_hi	E	Highest optimum environmental value
dest_x	M, E	Destination Longitude
dest_y	M, E	Destination Latitude
mot_x	M, E	Motivation (x direction)
mot_y	M, E	Motivation (y direction)
search_radius	M, E	Radius of semi-circular search region (km)
direction	M, E	Movement direction: N, S, E, W, or R (Random)
sigma	M, E	Randomness parameter
mortality	M, E	Incorporate agent mortality? T or F
fail_thresh	M	Deviation from optimum constituting failure
n_failures	M	Allowable number of failures before agent death
init_energy	E	Initial energy
energy_adj	E	Energy gain/penalty vector
single_rast	M, E	Using a single-layer raster? T or F
write_results	M, E	Save results as a csv? T or F
x	S	Origin longitude
y	S	Origin latitude
morphpar1	S	Morphological parameter num. 1 observed value
morphpar1mean	S	Morphological parameter num. 1 mean
morphpar1sd	S	Morphological parameter num. 1 SD
morphpar1sign	S	Morphological parameter num. 1 sign
morphpar2	S	Morphological parameter num. 2 observed value
morphpar2mean	S	Morphological parameter num. 2 mean
morphpar2sd	S	Morphological parameter num. 2 SD
morphpar2sign	S	Morphological parameter num. 2 sign

180

181 **Table 2.** List of arguments used in `moveSIM` (M), `energySIM` (E), or `as.species` (S). T: True,
 182 F: False, SD: standard deviation. In text, these arguments are presented in *italics*. For a more complete
 183 list of argument descriptions, see the `abmR` documentation.

184 The following algorithm applies when the argument *direction* is ‘N’, ‘S’, ‘E’, or ‘W’. For
 185 random movement (*direction* = ‘R’) agents simply select a random point from a circle of

186 radius *search_radius* for each timestep (Step 4). Here, let $env_rast(x_{t+1}, y_{t+1})$ be the value of
187 *env_rast* at the point (x_{t+1}, y_{t+1}) . The core algorithm shown here assumes that *env_rast*
188 contains no undefined (N/A) grid cells.

- 189 1. If morphological parameters are specified, compute adjusted motivations
190 ϕ_x and ϕ_y according to (3) and (4), respectively. If not, set $\phi_x = \phi_{x0}$ and $\phi_y = \phi_{y0}$,
191 where ϕ_{x0} and ϕ_{y0} are *mot_x* and *mot_y*, respectively.
- 192 2. Specify (x_1, y_1) using *x* and *y* contained in *modeled_species*.
- 193 3. Set failures = 0
- 194 4. For day *t* in 1:(*days*-1)
 - 195 a. Create a search area defined as a semicircle of radius *search_radius*
196 facing *direction* and centered at (x_t, y_t)
 - 197 b. Determine (ω_x, ω_y) as location within the search area with *env_rast*
198 cell value closest to *optimum*. Draw a random sample ($n = 1$) in case of
199 ties.
 - 200 i. If $(dest_x, dest_y)$ in search area, set $(\omega_x, \omega_y) = (dest_x, dest_y)$
 - 201 c. Large scale searching: determine $(x_{t+1}, y_{t+1})_0$ according to (1) and (2).
 - 202 d. Small scale searching: determine (x_{t+1}, y_{t+1}) by selecting location
203 within eight neighboring cells (queen's case) of $(x_{t+1}, y_{t+1})_0$ with the
204 cell value closest to *optimum*. Draw a random sample ($n = 1$) in case of
205 ties.
- 206 Perform (e)-(f) if *mortality* = True.
 - 207 e. If observed $env_rast(x_{t+1}, y_{t+1}) - optimum > optimum * fail_thresh$, set
208 failures = failures + 1. If not, set failures = 0.

- 209 f. If failures > $n_failures$, the agent dies. Set (x_{t+1}, y_{t+1}) through
210 (x_{days}, y_{days}) as N/A and end loop.
211 5. Return dataframe with $days$ rows and 2 columns movement track data.
212 6. Repeat (3)-(5) $replicates$ times.

213 **2.2. Simulation function: energySIM**

214 The function `energySIM` builds on `moveSIM` by allowing for dynamic agent energy levels
215 that are affected by the quality of environmental values achieved. These initial user-defined
216 energy levels then serve as a driver of mortality and movement distance per timestep. It
217 operates according to the following algorithm. Here, terms in *italics* are `energySIM`
218 function arguments (see Table 2) or calculated variables (e.g., *optimum*, *energy*).

219 The following algorithm applies when the argument *direction* is ‘N’, ‘S’, ‘E’, or ‘W’. For
220 random movement (*direction* = ‘R’) agents simply select a random point from a circle of
221 radius *search_radius* for each timestep (Step 5). Here, let $env_rast(x_{t+1}, y_{t+1})$ be the value of
222 *env_rast* at the point (x_{t+1}, y_{t+1}) . The core algorithm shown here assumes that *env_rast*
223 contains no undefined (N/A) grid cells.

- 224 1. If morphological parameters are specified, compute adjusted motivations
225 ϕ_x and ϕ_y according to (3) and (4), respectively. If not, set $\phi_x = \phi_{x0}$ and $\phi_y =$
226 ϕ_{y0} , where ϕ_{x0} and ϕ_{y0} are *mot_x* and *mot_y*, respectively.
227 2. Compute *optimum* as $(optimum_hi - optimum_lo)/2$.
228 3. Specify (x_1, y_1) using x and y contained in *modeled_species*.
229 4. Set *energy* = *init_energy*
230 5. For day t in $1:(days-1)$

- 231 a. If *mortality* = True, update *search_radius* as *search_radius* =
232 *search_radius* * (*energy/init_energy*).
- 233 b. Create a search area defined as a semicircle of radius *search_radius*
234 facing *direction* and centered at (*x_t*, *y_t*).
- 235 c. Determine (ω_x, ω_y) as location within the search area with *env_rast*
236 cell value closest to *optimum*. Draw a random sample (n = 1) in case of
237 ties.
- 238 i. If (*dest_x*, *dest_y*) in search area, set (ω_x, ω_y) = (*dest_x*,
239 *dest_y*)
- 240 d. Large scale searching: determine (*x_{t+1}*, *y_{t+1}*)₀ according to (1) and (2).
- 241 e. Small scale searching: determine (*x_{t+1}*, *y_{t+1}*) by selecting location
242 within eight neighboring cells (queen's case) of (*x_{t+1}*, *y_{t+1}*)₀ with the
243 cell value closest to *optimum*. Draw a random sample (n = 1) in case of
244 ties.
- 245 f. If *optimum_lo* < *env_rast*(*x_{t+1}*, *y_{t+1}*) < *optimum_hi* update *energy* =
246 *energy* + *energy_adj*[1].
- 247 g. Else, compute $\Delta = \text{env_rast}(x_{t+1}, y_{t+1}) - \text{optimum}$. And update energy
248 in the following way:
- 249 If $\Delta < 0.1 * \text{optimum}$, then *energy* = *energy* + *energy_adj*[2]
- 250 If $0.1 * \text{optimum} < \Delta < 0.2 * \text{optimum}$, then *energy* =
251 *energy* + *energy_adj*[3]
- 252 If $0.2 * \text{optimum} < \Delta < 0.3 * \text{optimum}$, then *energy* =
253 *energy* + *energy_adj*[4]

254 If $0.3 * optimum < \Delta < 0.4 * optimum$, then $energy =$
255 $energy + energy_adj[5]$

256 If $0.4 * optimum < \Delta < 0.5 * optimum$, then $energy =$
257 $energy + energy_adj[6]$

258 If $0.5 * optimum < \Delta < 0.6 * optimum$, then $energy =$
259 $energy + energy_adj[7]$

260 If $0.6 * optimum < \Delta < 0.7 * optimum$, then $energy =$
261 $energy + energy_adj[8]$

262 If $0.7 * optimum < \Delta < 0.8 * optimum$, then $energy =$
263 $energy + energy_adj[9]$

264 If $0.8 * optimum < \Delta < 0.9 * optimum$, then $energy =$
265 $energy + energy_adj[10]$

266 If $\Delta > 0.9 * optimum$, then $energy = energy + energy_adj[11]$

267 h. If $mortality = True$ and $energy = 0$, the agent dies. Set (x_{t+1}, y_{t+1})
268 through (x_{days}, y_{days}) as N/A and end loop.

269 6. Return dataframe with $days$ rows and 2 columns movement track data.
270 7. Repeat (3)-(6) $replicates$ times.

271 3. EXAMPLE APPLICATIONS

272 abmR can be used to construct ABM simulations for any desired agent across the globe. In
273 the following example, we demonstrate how `energySIM` can be used to compare the
274 movement and the differential energy allocation of two populations of 250 agents each.
275 While we focus on `energySIM` in this example, a similar workflow applies for `moveSIM`.

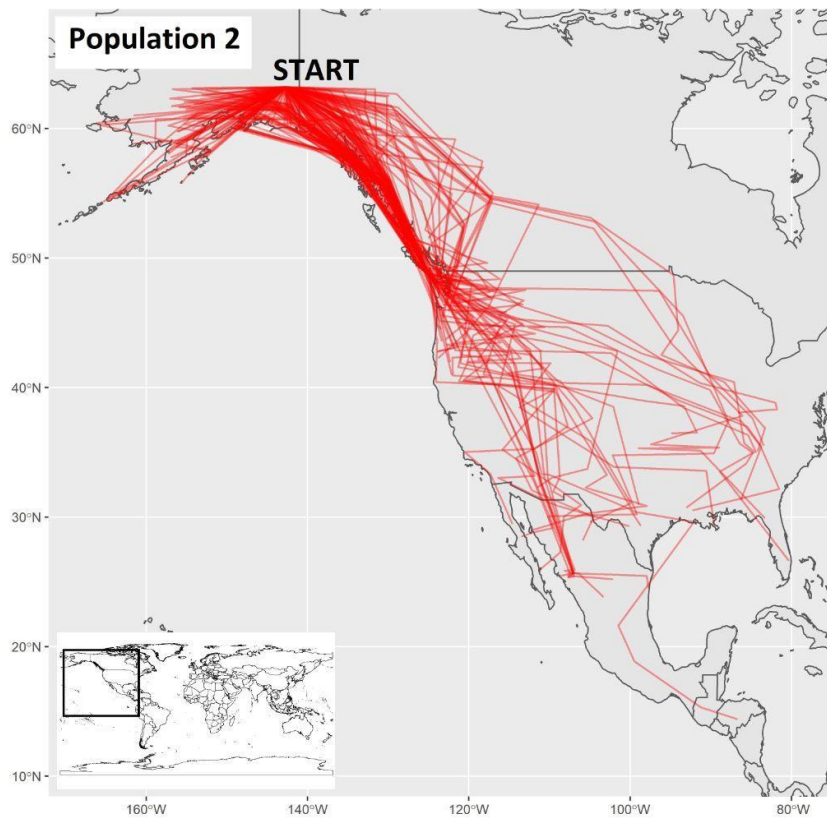
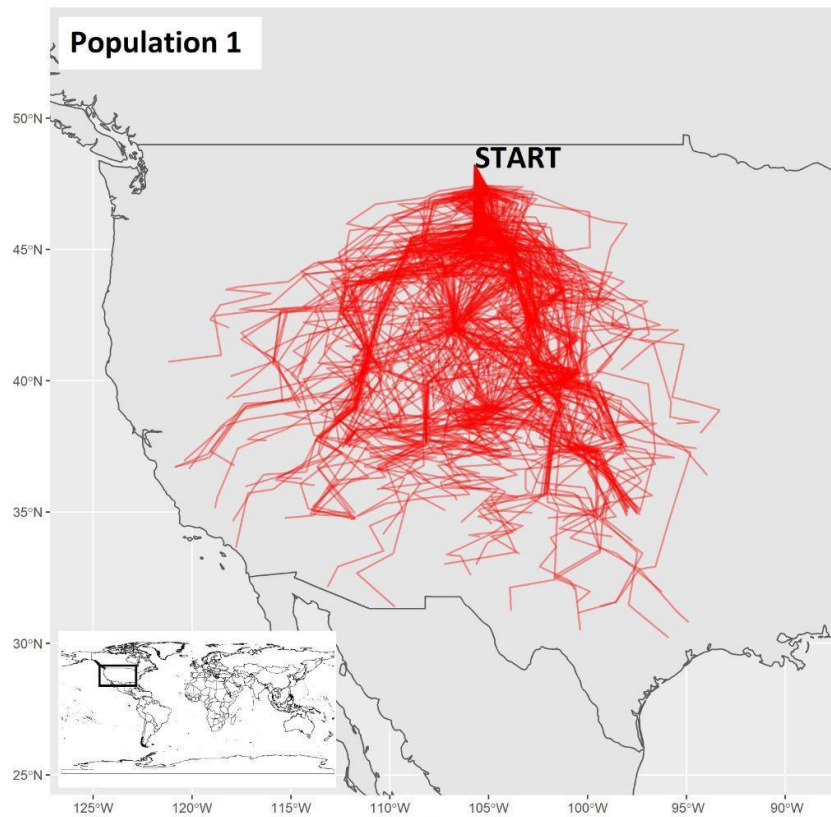
276 3.1. Comparisons between populations

277 In this example, both populations are characterized by the same number of replicates,
278 movement timesteps ('days'), the same σ , and the same environmental data provided by a
279 Normalized Difference Vegetation Index (NDVI) raster stack containing 14 days of data
280 between September 01-14, 2019 (Vermote, 2019). Both populations had an unspecified
281 destination (indicated with '999'). However, Population 1 (P1) agents started their
282 movements from a different point (105.7° W; 48.2 ° N) situated about 2,800 km from the
283 origin of Population 2 (P2) agents (142.7° W; 63.2 ° N). Additionally, P1 agents had a
284 smaller search radius (150 km) but higher motivation than P2 agents (P1 motivation = 0.95).
285 P1 agents also had different optimum ranges (P1 0.2-0.5; P2 0.6-0.8), and different initial
286 energy units (P1 100; P2 70). These differences in simulation parameterization result in
287 clearly dissimilar movement tracks (Fig. 3).

Population 1	Population 2
<pre>am.pop.1 = as.species(x = -105.7, y = 48.2) sim.move <- energySIM(replicates = 250, days = 14, env_rast = as.raster.stack.ndvi.sep, search_radius = 150, sigma = 0.1, dest_x = 999, dest_y = 999, mot_x = 0.95, mot_y = 0.95, modeled_species = am.pop.1, optimum_lo = 0.2, optimum_hi = 0.5, init_energy = 100, direction = "S", mortality = F, Energy_adj = c(20,10,8,5,2,0,-2,-5,-8,-10,-20), write_results = T, single_rast = F)</pre>	<pre>am.pop.2 = as.species(x = -142.7, y = 63.2) simtwo.move <- energySIM(replicates = 250, days = 14, env_rast = as.raster.stack.ndvi.sep, search_radius = 800, sigma = 0.1, dest_x = 999, dest_y = 999, mot_x = 0.8, mot_y = 0.8, modeled_species = am.pop.2, optimum_lo = 0.6, optimum_hi = 0.8, init_energy = 70, direction = "S", mortality = F, energy_adj = c(20,10,8,5,2,0,-2,-5,-8,-10,-20), write_results = T, single_rast = F)</pre>

289 **Box 1.** R code used for performing the simulations presented in Fig 3. First, `as.species` is called
290 to initialize two populations with different origin locations (here omitting morphology). Then,
291 `energySIM` is called to perform a movement simulation for each population; parameters that differ

292 between the two simulations are printed in red, functions in blue, and objects in bold. For argument
293 descriptions, see Table 2 and the package manual.



294

295 **Figure 3.** Movement tracks reveal that Population 1 tended to travel through the central United
 296 States, while Population 2 traveled mostly throughout western Canada, United States, and Mexico.
 297 Overall, Population 1 traveled more distance and exhibited more consistent paths near the origin than
 298 did Population 2. The movement tracks are natively produced by abmR. Inset world map provided for
 299 geographic reference.

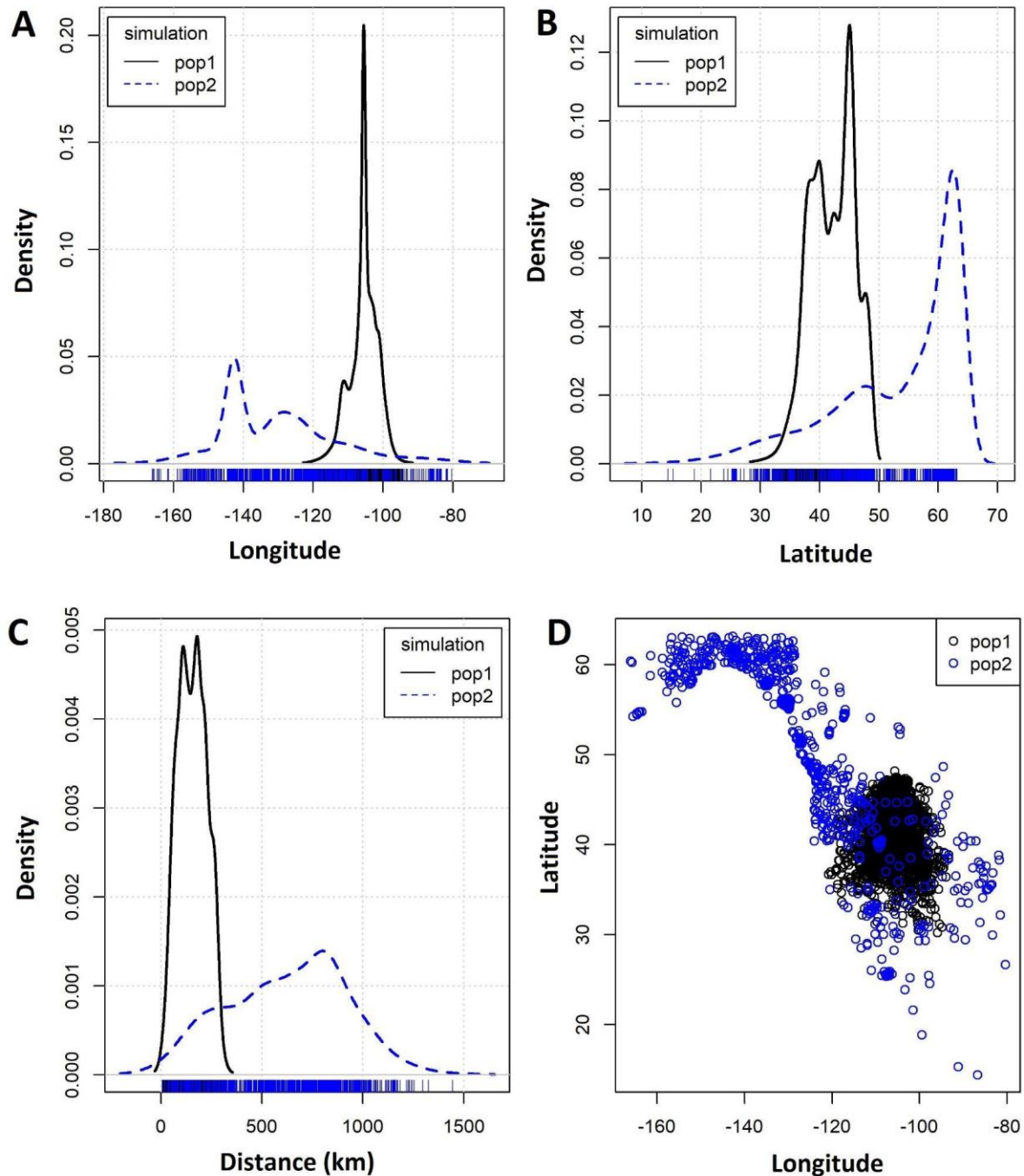
300 While we can compare the movement tracks visually, Table 3 provides a numerical
 301 description of results. In this simulation, P1 traveled a much smaller average distance (154.6
 302 km) than did P2 (625.5 km). However, P1 traveled more days on average (7.4 days) before
 303 stopping than P2 (3.8 days). Additionally, P2 had higher energy consumption than P1; its
 304 average remaining energy across all timesteps was 61.2 units compared to 99.7 units for P1.
 305 There are several possible reasons for this observed pattern. First, P2 began with a smaller
 306 initial energy (70 units) than P1 (100 units). Additionally, P2 had higher optimum NDVI
 307 values (0.6 - 0.8), which might have been less abundant and generally more difficult to reach
 308 than those of P1 (0.2 - 0.5). Finally, because they began in different places, P1 and P2 agents
 309 encountered different raster cells along their journey.

	variable	mean	sd	median	min	max	range
Population 1	day	7.4	4	7	1	14	13
	longitude	-105.5	4.1	-105.2	-121.1	-93.3	27.8
	latitude	41.6	3.4	41.9	30.2	47.5	17.3
	energy	99.7	1.3	100	80	100	20
	delta energy	-0.04	1.5	0	-20	20	40
	distance	154.6	70	154.4	5.5	316.7	311.1
	Population 2	day	3.8	3.08	3	1	14
longitude		-126	17.3	-127.1	-166	-80.3	85.7
latitude		50.2	10.5	52.2	14.4	63.1	48.7
energy		61.2	17.2	60	0	100	100
delta energy		-2.3	9.3	-5	-20	20	40
distance		625.5	294	649.7	5.5	1445	1439.4

310

311 **Table 3.** A numerical comparison of Populations 1 and 2, created by using values across all timesteps
312 for all agents. ‘Day’ summarizes the timestep variable of the movement tracks. ‘Longitude’ and
313 ‘latitude’ summarize the geographical position of agents, while ‘energy’ summarizes agents’
314 remaining energy. ‘Delta energy’ corresponds to the change (gain or loss) of energy between each
315 timestep, while ‘distance’ refers to the distance traveled between each timestep. This table was
316 produced outside of abmR using raw movement data returned by the package.

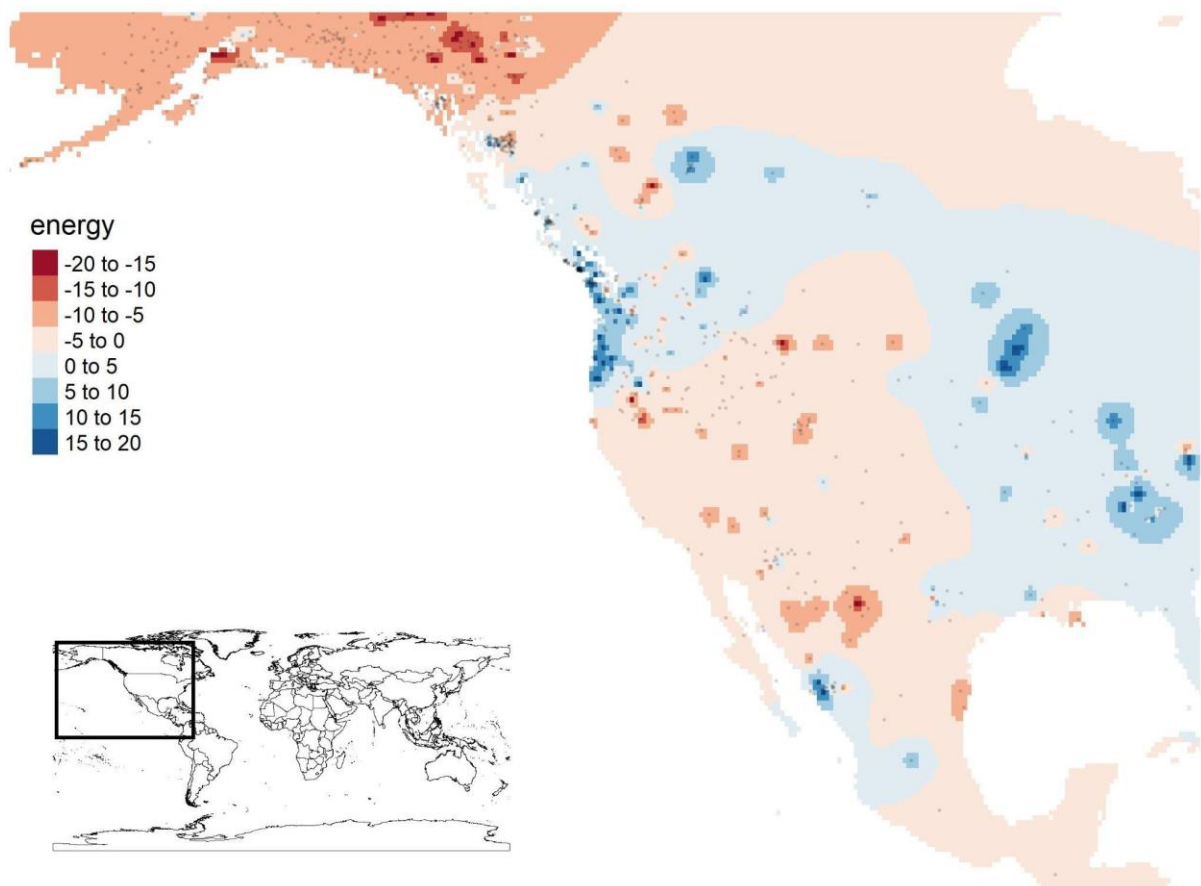
317 Fig. 4 visually compares P1 and P2 movement outputs based on longitude and latitude. This
318 is not a native abmR figure, but rather is produced using the raw data that abmR generates to
319 show the flexible use of the package. In this figure, P1 movements tended to be to the east
320 and south of P2. However, P2 trajectory shows a much wider distribution, with density points
321 extending to the lower values of latitude.



322

323 **Figure 4.** Graphical comparisons of Population 1 and Population 2 movements. Panels A and B show
324 density plots used to individually compare longitude (Panel A) and latitude (Panel B) coordinates
325 attained by agents from each population. Panel C compares the distance traveled between each
326 timestep, while Panel D shows geographical position for all agents in each population across all
327 timesteps.

328 Finally, Fig. 5 provides a density surface plot for P2 describing agent energy gains (blue) and
329 losses (red) across the landscape. This surface was created using the inverse distance
330 weighted interpolation (IDW) function from the R package ‘gstat’ (Pebesma, 2004). IDW
331 interpolates grid cell values across a surface using a linear combination of observed (sample)
332 points. When interpolating a cell value, the value of the sample points closer to that cell carry
333 a higher weight, while sample points further from that cell carry smaller weight. IDW is
334 discussed in more detail in Wong (2017). The results from Fig. 5 match well with what we
335 observe in Fig. 3. Movement tracks for P2 tend to follow the blue (energy gain) regions.



336

337 **Figure 5.** Energy gradient plot of Population 2 by timestep. Areas in red reflect energy loss (less
338 suitable environmental values) while areas in blue reflect energy gain (better environmental values).
339 This plot is produced directly by *energyVIZ*. Inset world map added for geographic reference.

340

341 4. CONCLUSIONS AND FUTURE WORK

342 abmR provides a novel and efficient programming platform for simulating large-scale
343 movements of species across taxa. We ran most of the initial test simulations on a local
344 machine equipped with an Intel® Core™ i7-5500U CPU – 2.40GHz and 8 GB of RAM and
345 obtained results for 100-1000 agents within minutes. The novelty of the software includes the
346 capability of concurrently modeling agent movement trajectories and energy budget. This
347 feature enables a broader exploration of the ecological constraints that shape animal dispersal
348 and/or migration. Moreover, abmR built-in arguments, such as *fail_tresh*, *n_failures*, and
349 *energy_adj*, provide additional flexibility when evaluating mortality scenarios that depend on
350 baseline environmental conditions and energy requirement during prolonged movement bouts
351 (see Table 2 for a full list of arguments affecting mortality).

352 Over the last decades, spatially explicit simulations and agent-based models have become
353 more popular in ecological and evolutionary studies (Railsback et al., 2006; DeAngelis &
354 Grimm, 2014). Analytical platforms, such as InSTREAM, a simulation model approach
355 designed to understand how stream and river salmonid populations respond to habitat
356 alteration (Railsback et al., 2009), or ALMaSS, a predictive modeling tool for answering
357 environmental policy questions regarding the effect of changing landscape structure on
358 threatened animal species (Topping et al., 2003), allow investigation of specific ecological
359 systems using ABM. On the other hand, many programming languages such as Netlogo, R, or
360 Python are widely used to develop custom and more flexible models that can be adapted to
361 address complex ecological or evolutionary research scenarios (Lustig et al., 2019; Chubaty
362 & McIntire, 2021). However, the use of a programming language to develop a flexible ABM
363 from scratch has two important drawbacks. First, it requires advanced programming skills.
364 Second, its reproducibility can be compromised by the idiosyncrasies of the simulation

365 algorithm written by the user. These idiosyncrasies, especially if not well documented, can
366 make it difficult or even impossible for other researchers to replicate findings or adapt code
367 to suit their modeling scenarios. `abmR` provides a novel framework to perform complex
368 movement simulations through standardized functions and arguments that facilitate model
369 annotation and reproducibility while providing publication-ready visualizations at the end of
370 each run.

371 While we developed and tested `abmR` as a movement and energy budget simulation tool, its
372 core software functionalities can be adapted to explore other processes such as disease
373 outbreak scenarios (Dougherty et al., 2018). As an example, pathogen vector movement can
374 be easily simulated within `abmR`, allowing the study of areas of confluence where disease
375 transmission is more probable (Manore et al., 2015). Moreover, potential future updates
376 include the ability to specify multiple raster stacks of different movement predictors and
377 different species traits affecting the movement patterns in the function `as.species`.
378 Additionally, other code expansions might be useful to study plant seed dispersal, interactions
379 of agents (density-dependent scenarios), and altitudinal movements.

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384 **Author Contributions**

385 B.G. led the development of the package and contributed extensively to the writing of the
386 manuscript; J.F.L. contributed to the package, writing, and critical review of the manuscript;

387 A.C. conceived the manuscript, led its writing, contributed to the package, and performed
388 package testing.

389 **Conflict of Interest Statement**

390 The authors declare that there are no financial or non-financial conflicts of interest.

391 **Data Availability**

392 abmR and the simulation results for Populations 1 and 2 are available for download from
393 Github at <https://github.com/bgoch5/abmR>. The environmental raster data used in the
394 examples is available at <https://www.ncei.noaa.gov>.

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